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EXOTIC SPECIES AND CONSERVATION

Research Needs

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OVER THE PAST TWO DECADES, EXOTIC INVASIVE SPECIES HAVE become recognized as an important cause of species declines and native habitat degradation (Vitousek et al. 1997; Wilcove et al. 1998). Although exotic species may increase species richness temporarily, over the long term they contribute to species extinction and therefore a decline in biological diversity. For years invasive exotic species were thought to be second only to land-use change in causing species extinctions (e.g., Soulé 1990; D'Antonio and Vitousek 1992), a claim now verified for fish (Miller et al. 1989), plants (D'Antonio and Dudley 1995), and threatened and endangered animal species in the United States (Wilcove et al. 1998). Approximately 60 percent of the species listed under the Endangered Species Act are threatened by invasive species (or fire suppression). Outside of the United States the proportion is estimated to reach 80 percent (Armstrong 1995; Wilcove et al. 1998). Crooks and Soulé (1999) predict that invasive species will soon become the leading cause of ecological degradation because of the increasing extent of disturbed lands, many of which are particularly vulnerable to domination by invasive nonindigenous species.

Exotic species threaten the persistence of native species assemblages because they can be predators, disease vectors, and competitors. They may so alter ecosystem processes that sustaining populations of native species or restoring ecosystem structure and function becomes difficult and expensive

(Vitousek et al. 1997). Although fewer than 20 percent of exotic species negatively affect native species or ecosystems (Simberloff 1981; U.S. Congress 1993; Williamson and Fitter 1996; D'Antonio and Haubensak 1998), this 20 percent can cause persistent changes to native biodiversity and ecosystem functioning. Species with this potential should receive the top priority for conservation and management efforts.

Despite increasing attention from conservationists and researchers, ability to predict establishment success and impact of nonindigenous species remains limited. In this chapter we suggest directions for research into the ecology of exotic species as they affect the conservation of native species and ecosystems. We focus on those issues for which quantitative biological research is needed to illuminate conservation challenges. For convenience, we divide research needs into (1) those addressing the ecology of invasive species, including pathways of introduction and factors affecting invasiveness, rates of spread, and impacts; and (2) those associated with their management, although we recognize the overlap. These research priorities are summarized in Box 4.1.

Factors Influencing Establishment and Spread

Trade and Pathways of Introduction

Humans have been a major vector of nonindigenous species from the beginnings of exploration, trade, and human migrations. Both the hulls and the holds of ships carry terrestrial and marine plants, animals, seeds, and disease between continents. Today, ballast water (the seawater a vessel takes on in one port, for ballast, and discharges upon arrival at another port) is an important source of introductions into marine and estuarine systems, carrying everything from cholera and botulism bacteria to invertebrates and fish. Estimates of the number of species carried in ballast water at any given moment range from 3,000 to 7,000 (Carlton 1999). We know little about invasion potentials and likely impacts of most of the species being transported.

Today, global trade, travel, and human migration have greatly increased rates of exotic introductions to all countries (U.S. Congress 1993; Mack et al. 2000). Although major pathways of introduction are well known, and many countries have established inspection and quarantine operations to monitor these routes for undesirable introductions, potentially dangerous organisms often arrive by previously unappreciated routes. We lack a comprehensive understanding of the many and varied routes through which introductions can occur.

Even when we are aware of potential pathways, we often do not have critical epidemiological information necessary to predict probabilities of establishment, such as the minimum numbers of individuals needed to establish a viable population and conditions promoting establishment and movement into native ecosystems. For example, numerous insects and plant pathogens have been found in association with wooden packing material, and the potential damage these species may cause to U.S. forests is well recognized (e.g., Wallner 1996). Much more information is needed on factors that affect establishment and spread of such species in order to develop more effective inspection and monitoring strategies. The risk of introduction is inherent in high trade volume, but we need to better evaluate acceptable levels of risk. Purposefully introduced species also have the potential to be directly problematic themselves or to be vectors of disease. Many are currently screened for associated disease organisms (e.g., White and Waterworth 1996), but the effectiveness of current screening and containment needs more research attention. Research on pathogen testing protocols could improve detection methods.

Undesirable exotic species also may be transported *within* a continent, greatly increasing the rate of spread, the exposure of potentially vulnerable ecosystems, and the magnitude of control problems. We need a better understanding of the relationships among pathway characteristics, frequency and abundance of propagule movements, and rates of invasive spread within continents to best direct policy and control strategies.

Predictors of Invasion and Spread

Species Traits and the Environment

Most exotic species do not become established in their new locales, although the small proportion that do become invasive may cause considerable ecological and economic damage. The attempt to identify common characteristics among those taxa that establish and spread on the one hand and among ecosystems vulnerable to invasions on the other has generated considerable debate. What kinds of species are most likely to invade particular types of ecosystems (Williamson and Fitter 1996; Levine and D'Antonio 1999; Lonsdale 1999; Newsome and Noble 1986; Stohlgren et al. 1999; Symstad 2000)? Because extirpation is close to impossible once an invasive has become established, ecologists are seeking better ways to predict which species are likely to become invasive and which ecosystems are most vulnerable to invasion (Ewel et al. 1999). Reliable predictors of invasibility are not yet available, in part because many models include species invading agricultural lands or other highly disturbed landscapes as well as those that invade natural areas (Parker and Reichard 1998). While establishment of many weedy plants is facilitated by disturbance, the process may differ for species that are invasive in native ecosystems (Hobbs and Huenneke 1992; D'Antonio et al. 1999). Likewise, the relative importance of ecosystem characteristics and disturbance in stimulating the establishment of animals is poorly known.

The most reliable determinant of potential invasibility into natural areas is whether a species has been invasive elsewhere. Reichard and Hamilton (1997) found that the best characteristic for predicting invasiveness among woody taxa in North America was whether the species had been reported to be invasive elsewhere. In the absence of a prior history of introductions, invasive potential must be evaluated based on a species' natural history or on the natural history of better-known congeners. However, congeneric species can differ greatly in their invasiveness, suggesting that the predictive capability of current models is not reliable. We need more information on traits correlated with successful establishment and spread and the circumstances under which they are likely to be important, particularly among closely related or ecologically similar species.

The history of intentional introductions of birds and biological control agents has shown that the number of times a species is introduced and the number of individuals per introduction attempt are the best predictors of successful establishment within the region (Newsome and Noble 1986; Hopper and Roush 1993; Crawley 1989; Veltman et al. 1996; Duncan 1997; Green 1997). Such intentional introductions generally have been made into highly modified ecosystems, like agricultural or urban landscapes. We have less information on correlates of success for exotic species entering native ecosystems. Nonetheless, a recent survey found that the rate of propagule arrival was an important determinant for the spread of exotic species into natural areas (Lonsdale 1999). A regular source of propagules greatly increases the likelihood of spread for many reasons. Small populations of colonists are at risk due to Allee effects, genetic bottlenecks, and the high likelihood of stochastic population extirpation (Williamson 1996). In addition to overcoming genetic or breeding problems, a high rate of propagule rain increases the chance of propagules encountering favorable habitats. D'Antonio et al. (in press) suggest that given high propagule supply rates and suitable climate conditions, virtually any ecosystem may be vulnerable to the establishment of exotic species. Research is needed to determine the circumstances under which factors contributing to population or community resistance can be overwhelmed by high rates of propagule arrival.

Although stochastic natural events can be responsible for establishment failure, they can also contribute to the success of an invader. For example, during the 1989–92 drought in England, river flow dropped sufficiently to allow the Asian mitten crab (*Eriocheir sinensis*), which had long been established at the river mouth, to migrate upriver and become established there. Ironically, even beneficial environmental changes, such as reduced pollution, can facilitate invasion by nonindigenous species that are present in low numbers. Populations of the wood-boring gribble (*Limnoria tripunctata*) exploded in the Long Beach–Los Angeles Harbor in the late 1960s because of pollution reduction, even though the isopod had been present in the harbor prior to the 1900s (Crooks and Soulé 1999 and references therein). Given widespread effects of chemical pollution, climate change, and alteration of nutrient cycles, it is essential that we develop models to anticipate movement of nonnative species across the landscape as a consequence of global change. This may be particularly important for disease organisms whose hosts (presumably native species) may be weakened by environmental stresses.

Until recently, low-diversity simple systems were thought to be most vulnerable to biological invasions (Elton 1958; Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999). Recent analyses suggest, however, that invasions are more likely in regions where species diversity is high (Levine and D'Antonio 1999; Stohlgren et al. 1999; Levine 2000; Stadler et al. 2000). These results are contrary to theory, which holds that high species diversity confers resistance to invasion because resources are more fully used (see Levine and D'Antonio 1999 for a review). However, the same environmental conditions that favor diversity of native species (e.g., high resource availability) may also favor exotic species (Stohlgren et al. 1999; Levine and D'Antonio 1999; Levine 2000; Stadler et al. 2000).

As a result, two relatively new hypotheses have emerged: (1) The most diverse communities may in fact be the most vulnerable to invasion, and (2) species losses from diverse communities may lower their resistance to invasion. The correlation between high diversity and high invasibility suggests also that relatively resource-poor ecosystems are at less risk of invasion. Richardson et al. (2000) suggest that in resource-poor environments invasions may be facilitated by mutualisms either between native species and invaders or between previously established and newly arriving invaders. In parts of the tropics, low rates of invasion have been attributed to resource exhaustion and lack of mutualisms, rather than to competition or community resistance (Richardson et al. 2000; Stadler et al. 2000), but experimental evidence in support of these hypotheses is lacking.

The importance of diversity (and species interactions) to invasibility can vary with spatial scale (Levine and D'Antonio 1999; Planty-Tabacchi et al. 1996; Stohlgren et al. 1999; Symstad 2000; Levine 2000; Wiser et al. 1998). For example, Stohlgren et al. (1999) and Levine (2000) found that only at their subplot and plot levels were the most diverse ecosystems resistant to plant invasions. The relationship between neighborhood mechanisms and community patterns relative to invasions rarely has been examined.

Time Lags during Invasion

The detection of a biological invasion may be delayed considerably after the event because the initial population size is small and difficult to detect. In addition, some populations may exhibit an extended lag period before population growth becomes explosive (Crooks and Soulé 1999; Hobbs and Humphries 1995; Schmitz and Brown 1997; Mack et al. 2000). Despite the apparent commonness of this phenomenon, its causes are not well understood. Among the potential mechanisms contributing to such lags in population growth are slow intrinsic growth rates of the invader, the occurrence of environmental changes promoting more rapid growth rates, the occurrence of genetic changes leading to higher rates of reproduction (Crooks and Soulé 1999), and the continued introduction of new colonists.

For example, the explosive growth of *Melaleuca* into new Florida habitats may have occurred following a genetic mutation allowing broader environmental tolerance (Ewel 1986; Crooks and Soulé 1999). Richardson et al. (2000) suggested that a long lag phase may reflect the absence and subsequent establishment of a necessary symbiont. For example, pines did not become invasive in the southern hemisphere until human activities distributed spores of ectomycorrhizal fungi, which facilitated the naturalization of the pines (Richardson et al. 2000). Because many mutualisms are nonspecific, an invader may benefit from symbionts not found in its native habitat (Richardson et al. 2000). Other cases of seemingly sudden explosive growth can occur when grazing pressure is reduced by removal of herbivores. On Santa Cruz Island in Southern California, fennel (*Foeniculum vulgare*), an introduced European perennial species, was present but not widespread until introduced cattle and feral sheep were removed as part of a conservation effort. Upon removal of the grazers, fennel grew explosively and is now dominant on more than 10 percent of the island (Crooks and Soulé 1999). Despite the enormous potential impacts of introduced disease organisms on native species and ecosystems, we know almost nothing about rates of population increase after introduction or factors influencing apparent lags or the onset of exponential growth. Because control is more likely when populations are small, it is essential that we understand the nature of the lag phase and factors that affect its duration.

Importance of Genetic Diversity to Invasion

Since the classic publications of Baker and others (*Genetics of Colonizing Species,* Baker and Stebbins, 1965), there has been long-standing interest in genetic changes occurring in populations during expansion stages and the importance of genetic diversity to invasion. Several investigators have demonstrated that species with low genetic diversity can become widespread invaders (e.g., Raybould et al. 1991; Stiven and Arnold 1995), while others have found that high genetic diversity occurs in many widespread invaders (e.g., Novak et al. 1993; Demelo and Herbert 1994). More information is needed on the circumstances under which intraspecific genetic diversity promotes or restricts invasion and the relative importance of phenotypic plasticity in allowing widespread invasion in species populations with low genetic variability. Hybridization between invaders and closely related congeners can also accelerate invasion (Vila et al. in press; Daehler and Carino in press).

Impacts of Exotic Species on Native Species, Communities, and Ecosystems

Because exotic species can affect many properties of native populations, communities, and ecosystems, it is difficult to suggest simple and/or comparable measures of impact suitable for use in different ecosystems. Parker et al. (1999) argue that we need a common currency by which to assess species impacts so that investigators can more easily compare their findings and concerns, and species can be more easily prioritized for control. Here we consider effects of exotic species on the likely persistence of native species to be the primary currency of concern. Very few countries recognize ecological pests as species whose movements should be controlled, and species can pass unimpeded into many countries as long as they are not known to be agricultural pests. Quantitative information is badly needed on the potential for ecological damage of many species, particularly those that are being actively traded in the horticultural or pet trade and those that come along as hitchhikers.

Genetic Effects

Invasive, non-native species can affect native species populations through hybridization. Introgression of genes from non-native species can lead to the almost complete loss of the native gene pool. This kind of "genetic swamping" can lead to extinction of a rare species (Levin et al. 1996; Rhymer and Simberloff 1996). Fisheries studies provide a clear example of how this can occur at the subspecific level. Both exogenous and artificially reared Atlantic salmon (*Salmo salar*) have been released for more than a century (Hindar et al. 1991). These releases overwhelmingly have reduced fitness of native populations regardless of whether the introduced salmon were wild or cultured. Salmonid populations are considered to be genetically adapted to their local environments, and hybridization with cultured salmon has disrupted local gene pools (Hindar et al. 1991).

Numerous examples have been documented of this mechanism of loss or change within a native taxon, particularly in animal species (Miller et al. 1989; Rhymer and Simberloff 1996; Vila et al. 2000). Despite published information documenting such impacts, interspecific hybridization or hybridization among subspecies is generally ignored as a serious threat to native species. So-called native species from nonlocal gene pools are commonly used in restoration, revegetation, and landscaping projects. Yet we know little about the degree to which these represent a genetic threat to the persistence of native genotypes or subspecies in the surrounding landscape or the degree to which local adaptation of native species even occurs or can be disrupted. Knapp and Rice (1996, 1998) found that the two native grasses most commonly planted in restoration projects in California, *Nassella pulchra* and *Elymus glaucus,* show high among-site genetic heterogeneity and local adaptation. They also found that restoration practitioners were likely responsible for the movement of genotypes around the state to locales distant from their place of origin (E. Knapp, personal communication) and caution that seed collection zones may need to be very restricted for some species to avoid genetic contamination (Knapp and Rice 1996).

The extent to which these exotic genotypes will decrease the fitness of local genotypes is not known. In at least one instance (*Phragmites australis* in the eastern United States), the introduction of an exotic genotype has led to a native species becoming more invasive, with potentially undesired impacts on wildlife habitat (Crooks and Soulé 1999; Chambers et al. 1999). In many cases interspecific hybridization has been demonstrated to contribute to the formation of more invasive genotypes, which then replace both native species and the original invader (Thompson 1991; Ayres et al. 1999).

Population, Community, and Ecosystem Impacts

Invasive exotic species can cause the decline of native species directly through competition, predation, or disease, or by altering ecosystem processes such that native species begin to die out. Predicting species impacts depends on understanding how traits of the invading species operate under the circumstances of the recipient ecosystem. Impact quality and quantity are affected by the abundance of the invasive species, its particular traits (e.g., rates of food consumption or resource uptake), and characteristics of species in the invaded community. Very few studies quantify impacts of plant invaders, and no systematic review of species traits and their population or community-level impact has been carried out.

Most extinctions caused by species invasions have been due to the introduction of predators of a size (e.g., Nile perch in Lake Victoria) or a feeding type (e.g., snakes in Guam) with no historical precedence in the invaded ecosystem. Pathogenic organisms also have caused extinctions (e.g., avian malaria in Hawaii), presumably when native species lack appropriate resistance. By contrast, exotic species that merely compete with native species contribute to species declines (e.g., Daehler and Carino 1999) but appear less likely to cause extinctions by themselves (Frankel and Soulé 1981).

Vitousek (1990) suggested a conceptual framework for predicting when the addition or deletion of a species is likely to have an ecosystem impact. He predicted that species causing ecosystem impacts are those that (1) introduce a new trophic level to the system, (2) alter the rate of resource supply to the system, or (3) alter the disturbance regime. Similarly, Chapin et al. (1996) suggest that species affecting ecosystem processes have traits that are qualitatively different from the native species in the invaded sites. They and others (Mack and D'Antonio 2001) predict that invaders whose traits differ only quantitatively from native species will affect native species largely through competitive interactions. Some effects on ecosystem processes and community structure may take many years to be manifested. Selective comparisons—e.g., of the impacts of an invasive through a range of invaded habitats, or of the impacts of different kinds of invaders—will be particularly useful to elucidate these ideas.

In addition, we have an urgent need to understand how impacts at one trophic level will translate to other levels. Pathogens such as plant diseases and animal viruses can reduce the abundance of their hosts quickly (see chapter 8). If these species interact strongly with other species—e.g., are important sources of food or shelter—their elimination could be catastrophic for entire communities.

While there has been much debate about the relationship between species diversity and community susceptibility to invasion, there has been little discussion of how native diversity moderates the *impacts* of exotic species. On the basis of his observation that introduced species had large impacts on island ecosystems, Elton (1958) suggested that more simple (and therefore presumably less diverse) ecosystems were more likely to be affected strongly by nonnative species. Simberloff (1995) and D'Antonio and Dudley (1995) likewise found that extinctions caused by invasive exotic species were more common on island ecosystems originally lacking some functional groups. However, there have been few studies of the relationship between diversity and the impact of invaders in continental ecosystems, particularly where diversity within and among functional groups or trophic levels is manipulated.

If invading species interact with natives primarily through competition for limited resources, removal of the exotic should produce a compensatory increase in native populations if propagule supply is not limited. If so, then impacts of exotics should be reversible in the course of a restoration program. However, if invaders alter ecosystem processes such as disturbance regimes or soil processes, impacts may not be readily reversed. For example, the introduction of fire-enhancing grasses to semi-arid ecosystems has greatly increased fire frequency in many ecosystems (D'Antonio and Vitousek 1992). Grass populations are not controlled easily nor are grass-fire cycles easily interrupted. In addition, the changes caused by the altered disturbance regimes are not easily reversed. More research is needed to determine the types of impacts that are reversible and the relationship among traits of the invaders, likelihood of control, and reversibility of impacts.

Effects and Invasiveness of Genetically Modified Organisms

Genetically modified organisms (GMOs) are produced by the insertion of genes into or the removal of genes from a target organism to confer more desirable or delete undesirable traits. This technology has been used in place of traditional plant breeding programs, for example, to significantly decrease the development time for commercial varieties of crops or to increase resistance to herbivores (Paoletti and Pimentel 1996). Several ecologists have pointed out that the release of GMOs is analogous to the introduction of exotic species (Levin 1988; Parker and Kareiva 1996). An important question in terms of conservation biology is whether GMOs will invade natural ecosystems, hybridize with related species, and/or in some way threaten native populations and communities (Raybould and Gray 1994; Parker and Kareiva 1996; Beringer 2000; Hails 2000). Concern has also been raised that wild animal populations will be attracted to pollen produced by a genetically modified crop but will be killed by compounds such as insecticides that are produced by the crop (Poppy 2000). There are almost no ecological data to bring to bear on the controversy.

There has been considerable alarm among the public over the introduction of genetically modified organisms, particularly in Europe. While it is generally assumed that most intentional introductions of GMOs will be benign, it is also acknowledged that some risks exist, since novel genotypes will be created and introduced to environments that are new to them (Levin 1988). In the United States, companies that want to commercialize genetically modified crops are required to show that their product will not become more of a pest species than its unaltered counterpart. However, these requirements are not considered to be rigorous enough by some ecologists, since it can be very difficult to anticipate the invasiveness of particular species or genotypes (Purrington and Bergelson 1995) or to anticipate the rate of pollen movement between GMOs and wild relatives. Considerable doubt surrounds the successful prediction of invasiveness based on the examination of DNA sequences, especially because thus far progress has been limited in predicting invasiveness based on factors better understood than DNA, such as character traits (Purrington and Bergelson 1995; Bergelson 1994; but see Rejmanek 1996).

Experimental and observational work to date does suggest that GMO pollen will spread to wild populations (e.g., Timmons et al. 1995; Lefol et al. 1996), but the extent to which this will occur or is a threat to native populations is debated (Salisbury 2000; Wilkinson et al. 2000). The potential "weediness" of GMOs themselves is also controversial. In a set of experiments with *Arabidopsis thaliana,* Bergelson (1994) found that the genetically altered genotypes bred for herbicide resistance produced fewer seeds and thus had reduced fitness relative to wild-type genotypes. They were nonetheless equally as weedy as their wild relatives. She interpreted this outcome as being the result of population size being limited by something other than seed number. A broad conclusion from this work is that field experiments under a variety of conditions are necessary to ascertain the true ecological risks associated with GMOs (Bergelson 1994).

From an ecological point of view, a significant flaw in the testing of GMOs for commercial release has been the failure to determine whether these species will become invasive if they escape to natural areas. Such testing would require experimentation under a range of realistic field conditions, and this is rarely done. In addition, weeds that are already present in a system are equally likely to benefit from the new traits such as herbicide resistance, insect resistance, stress tolerance, and the ability to fix nitrogen. For example, there is the potential introgression of herbicide resistance to closely related species that are already considered "weedy," making management even more difficult (Hails 2000). Further, reciprocal hybrids of crops and wild species must be studied even if they do not exist in the country where the GMO originated, since some countries that receive GMO products may be home to the wild relatives, and many countries may lack sufficient regulations and/or resources for proper screening (Purrington and Bergelson 1995).

While genetically modified crops might have some environmental benefits because they reduce the need for the use of herbicides and pesticides (Beringer 2000), the topic remains highly controversial among ecologists and the public alike. At a minimum, more rigorous experimental testing, as well as limiting use of GMO crops to areas where no wild relatives are found, will help to reduce the risk of genetically engineered plant invaders (Barrett 2000).

Control of Invasive Species and Restoration of Communities and Ecosystems

Limited resources and lack of consensus by land managers, conservationists, and the general public mandate that we develop a better understanding of the biological and economic consequences of prevention, mitigation, and control measures against invasive species. Potential control mechanisms include import restrictions, mechanical and chemical control programs, and the use of other exotic species to reduce target species and restore environments and communities. Ultimately, the allocation of resources for invasive species management and the protocols through which such management is implemented are matters for public debate and resolution. In many cases, however, we lack both the factual and the theoretical basis with which to inform those discussions. We will need a broad understanding of the consequences of both action and inaction in the application of control protocols on which to base appropriate risk analyses.

Fundamental ecological information is necessary for developing priorities for exotic species removal, control, or use (see above). For example, development of reliable risk analyses will require more extensive research into the combination of species characteristics, community composition, and ecosystem processes that lead to explosive population growth; a better understanding of the impacts invasive species have on community and ecosystem characteristics; and research into the relative roles of propagule availability, resource supply, and community structure in determining establishment rates of both exotic and native species.

Such information will form the necessary foundation on which to develop priorities for exotic species management in natural ecosystems. Many naturalized exotic species may not threaten native species or compromise management goals (Williams 1996). In Hawaii, of more than nine hundred exotic species naturalized in native communities, less than 10 percent are seen as presenting a current threat to native species or ecosystem processes (Wester 1992). However, invasive species may persist at low population levels for many years before explosive population growth brings them to the attention of managers (Crooks and Soulé 1999), yet control is more easily effected while populations and ranges are small.

Even where ecological impacts of invasive species are substantial, their removal or control is likely to be only part of a long-term management program. Reestablishment of native communities is rarely accomplished by elimination of an invasive exotic. Seed stocks may be lost, disturbance regimes may be altered, and high resource availability after the disturbance associated with removal may favor establishment of other exotics. A substantial part of community structure may depend on timing and opportunity for establishment, and biotic structuring forces may be overwhelmed by seed inputs from exotic species. Removal or reduction of a dominant exotic may not reestablish critical ecosystem processes such as disturbance regimes (Adler et al. 1998; Cabin et al. 2000; Mack and D'Antonio 1998), soil chemistry (Macdonald and Richardson 1986; Vivrette and Muller 1977; D'Antonio 1990; Vitousek et al. 1987), and hydrology (Lacey et al. 1989). Experimental studies of the removal or reduction of exotic species would contribute to understanding of their impacts and of processes affecting subsequent community structure and ecosystem processes (Morrison 1997). Priorities for exotic control should include projections of the composition and structure of the post-removal community, yet the consequences of control are poorly understood and are often not anticipated. Under what circumstances does control or removal of an invasive species reverse its impact or lead to a less desirable condition?

Although exotic species are often introduced intentionally for habitat restoration and invasive species control, our understanding of the risks involved is limited. Cover crops are used as part of large-scale restoration efforts to slow environmental degradation, reduce erosion, improve soil structure and nutrient supply, moderate microclimates, and alter disturbance regimes (NRC 1993; Richardson 1999). Selected species are often exotics, because cultural information on native species may be wanting, seed supply may be insufficient, or native species may not possess the appropriate characteristics for the intended purposes. Although native species may establish under such cover crops (e.g., Parotta 1992; Lugo 1992), exotics also may retard early seedling establishment, persist as a semipermanent component of the landscape, and in some cases become invasive as well. *Leucaena leucocephala,* a nitrogen-fixing legume, was broadcast aerially over Guam and Saipan to control erosion following the devastating World War II bombardment; fifty years later, the northern portion of the island is dominated by this early successional species, and native forests are much restricted in distribution. Moreover, Richardson (1998, and references cited therein) offers evidence that tree species that cause the greatest problems as invasives are those that have been most widely planted for the longest period of time, suggesting that under appropriate circumstances most widely planted trees in alien environments are likely to become problematic.

Predators, herbivores, and pathogens from their native ranges may be introduced as control agents for invasive species. Biological control often offers the only viable option for reducing populations of widespread exotics, for which it provides a low-cost method with relatively low impact on native ecosystems (Odour 1999). Although the risk of adverse impact on nontarget species has been reduced from the early days of biological control, when introductions were accomplished with less research and the value of nontarget indigenous species was less appreciated (Simberloff and Stiling 1996; Howarth 1991), appropriate pre- and post-release research on impacts to native species and communities is relatively recent. The unique combinations of species, environment, and community that characterize any introduction of an exotic species make predicting the consequences difficult. Higher-order interactions (parasite-host interactions, pollination systems, trophic structures) are particularly difficult to predict in advance (Memmott 1999). A better understanding of the consequences of such introductions based on field and lab experiments in habitats of origin and introduction would provide a better basis for assessing risk.

BOX 4.1. Research Priorities for Invasive, Non-Native Species and Their Potential Impacts on Natural Populations and Communities of Ecosystems

Investigate Pathways of Introduction:

†1. What are the critical pathways of introduction of new species, and how do they differ in contributing harmful nonindigenous species? For example:
   - † Introduced plant pathogens can have devastating consequences for entire ecosystems. What are the most important pathways for their arrival, and how do they subsequently spread?
   - † Introduced insects may also strongly affect forested ecosystems and may carry pathogens. What are the most common pathways for harmful nonindigenous insect species to arrive in new locales, and how does the likelihood of their successful establishment scale with volume of trade?

†*2. What are acceptable levels of risk of entry of known potential invaders, how well do protocols established to prevent accidental introductions really work, and how can protocols be improved?

3. How do minimum viable population sizes of invaders vary among species, ecosystems, and establishment circumstances? Are there useful generalizations to be made here that might help development of monitoring and screening strategies?

†*4. Under what circumstances do intentional introductions for commercial purposes contribute to the introduction and spread of harmful invasive species? Can we develop reliable risk assessment protocols to screen intentional introductions for potential invaders, particularly harmful ones ?

Investigate the Processes of Invasion and Spread

1. What traits characterize species with high potential for rapid spread beyond their site of introduction?

2. What are the characteristics of natural communities that affect their resistance to invasion? How does propagule pressure interact with resistance, and under what circumstances can we expect propagule pressure to overwhelm resistance?

*3. How will the spread of non-native species be affected by other global changes, such as chemical pollution, climate change, altered disturbance regimes, and alteration of biogeochemical cycles? For example:
   - Will nitrogen deposition increase rates of plant invasions by favoring fast-growing non-native species?
   - Will changes in storm frequencies and intensities affect the persistence of native populations and potentially favor disturbance-loving exotic species?
   - Will increasing environmental stresses such as air- or water-borne pollutants make native species more susceptible to introduced diseases?

†4. Why are tropical ecosystems less invaded by nonindigenous species than their temperate counterparts? Will increasing fragmentation of tropical habitats and propagule pressure from exotic species alter this pattern?

5. What is the relationship between neighborhood-scale species interactions that affect invader success and landscape-level patterns of invasion and impact?

*6. Why are there often long time lags between establishment and the explosive growth and spread of introduced populations? Are there commonalities among species in their invasion patterns relative to the occurrence of time lags?

7. How does genetic diversity influence rates or patterns of invasion?

†8. How do human activities and cultural patterns—e.g., road construction, land-use patterns, traditional uses of plants, and visitation to reserves—affect the introduction and spread of invasive species?

Assess Impacts

†*1. What is the potential for introgression of introduced genes to native species, and under what circumstances is this likely to cause a change (either positive or negative) in fitness (and hence ecological performance)? How does the likelihood of such introgression vary among mating systems and life history characteristics of introduced taxa?

2. What traits of exotic species increase the danger of genetic threats to native species? What ecosystem characteristics are associated with high rates of genetic introgression?

3. Which species traits (or combinations thereof) are most likely to threaten local persistence of native species or create difficult-to-reverse impacts on ecosystem processes?

4. Does the arrival and establishment of one or a few non-native species influence the establishment of further alien species?

*5. How can knowledge of species traits be overlain or interfaced with ecosystem traits to predict species impact?

6. What kinds of higher-order effects—e.g., on other trophic levels or on community processes—are associated with interspecific interactions involving introduced species?

7. How do species richness, functional diversity, and trophic complexity influence the impact of an invader?

*8. Under what circumstances are impacts of an invasive species likely to be reversible? Are ecosystem effects longer lasting or farther reaching than competition or predation effects? Are impacts due to competition or predation more likely to cause population declines or extinction among native species?

(*continues*)

BOX 4.1. (*Continued*)

Consider Genetically Modified Organisms

†1. Under what circumstances might GMOs or their genes be able to spread beyond points of introduction?
†2. Under what circumstances might the spread of GMOs or their genes into wildland habitat pose a threat for native species or ecosystem structure and function?
†3. What criteria are needed to develop protocols for release and risk assessment associated with GMOs?

Study Control, Restoration, and Their Interactions

†1. How do we develop priorities for exotic species removal, control, or use?
2. Under what circumstances does control or removal of an invasive species lead to a less desirable condition?
3. Under what circumstances is the introduction of exotic species warranted for restoration or for biological control of invasive non-native species?

Note: An asterisk indicates a top research question. A dagger indicates a research priority that needs an answer within next ten years, or it will be too late for many species or natural communities.

Concluding Remarks

Native biological diversity is valued for many reasons. Its preservation is one of the major challenges of this century. Invasive nonindigenous species contribute to this challenge because a small but significant fraction of them interfere with native species and contribute to their demise on a local or even global scale. Some alter ecosystem processes such that there is a complete alteration of community composition, structure, and function. To reduce the risk of introduction and spread of harmful invaders and better manage existing nonindigenous species for the benefit of native biological diversity, we need greater access to basic information on their ecology and the ecology of the potential systems they might enter. In addition, we need greater coordination among agencies and institutions conducting that research and coordinated development of databases that can be made available to managers.

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